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illustrates the general truth that we, like the birds, have but a very limited power of altering the ebb and flow of our behavior cycles. Cyclical recurrence does not prove that human behavior consists of mere chain reflexes, neither does it prove that the instinctive behavior of birds consists of mere chain reflexes.

Doctor Raymond Pearl read a preliminary draft of this paper and suggested important improvements, for which I express my thanks.

The article of which this is an abstract will appear in the *Biological Bulletin*.

¹ Herrick, C. J., *Introduction to Neurology*, 1915, (61).

² Thorndike, E. L., *The Original Nature of Man*.

³ Ellis, H., *Studies in the Psychology of Sex. III. Analysis of the Sexual Impulse*.

⁴ Hirn, Y., *The Origins of Art*.

RAPID RESPIRATION AFTER DEATH

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Communicated by G. H. Parker, October 20, 1917

Various observers¹ have reported that respiration may continue after death but apparently the rapidity of post mortem respiration does not in any of these cases exceed the normal rate. It is therefore of interest to find that the marine alga *Laminaria* in the presence of certain reagents may respire more rapidly after death than in its normal state.

In my experiments the rate of respiration was determined by measuring the output of CO₂ (at 16°C.) by means of suitable indicators added to the solution which had been rendered acid by the respiration of the *Laminaria*. The method has been previously described.²

As soon as a determination of the respiration had been made, the solution bathing the tissue was renewed and after exposure for the same length of time the amount of respiration was again determined. In this manner the respiration of the material could be followed and it could be seen whether it was approximately constant before the beginning of an experiment. This constancy was obtained in all the experiments here recorded.

In some cases (acetone 17.4% and alcohol 24.2%) the killing agent extracted from the plant a small amount of pigment which interfered with the color of the indicator.³ But this difficulty disappeared after the first two periods, as was shown by running pure hydrogen through the solution, after which it returned to the color found in normal sea water plus indicator. This method also showed conclusively that the acid excreted by the plant was CO₂ and not an organic acid.

The methods of killing the tissue were various. Sea water containing anesthetics (made up to the conductivity of sea-water by the addition of concentrated sea-water) was employed in many of the experiments. In this case the respiration was determined for several periods of equal length in sea-water (the solution being renewed after each period). The sea-water was then replaced by sea-water containing anesthetic and the respiration determined after successive equal periods until death ensued, and for some time thereafter.

As it was important to know the time of death as accurately as possible, determinations of the electrical conductivity of the tissue were made by the method of Osterhout.⁴ If the electrical resistance of the normal tissue be called 100% it is found that on killing the resistance falls to about 10%. When the resistance has fallen to 15% the tissue is for all practical purposes dead, as there is no recovery when it is returned to normal conditions.

It was found that with sea-water approximately saturated with ethyl bromide the rate of respiration was about doubled. After the tissue was dead (as shown by the electrical resistance) it continued to respire for some time at a rate above the normal. Somewhat similar results were obtained when the sea-water contained 17.4% of acetone (by volume) and was made up to the conductivity of sea-water by the addition of concentrated sea-water. In this case the post-mortem rate of respiration is far above the normal and remains so for about 2 hours after the death of the tissue. This is also the case with sea-water containing 24% (by volume) of ethyl alcohol (the solution being made up to the same conductivity as sea-water).

With sea-water which contained 3.2% formaldehyde, (the free acid neutralized with sodium carbonate and the solution made up to the conductivity of sea-water) it is found that at the end of 100 minutes after the electrical resistance shows the tissue to be dead, the rate of respiration has fallen to normal (before this time the rate is much above the normal).

Experiments were made to ascertain whether different methods of killing would give different results. Tissue was exposed to running tap water for 19 hours (which was longer than was required to kill, as was shown by the electrical resistance). After the exposure, the respiration rate was too small to be detected. It is probable that in this case the rise and decline of the rate of respiration was completed before the end of 19 hours.

The respiration of another lot of material was determined before and after killing by means of exposure to a large volume of sea-water at

35°C. for 70 minutes (the time, as found by determining the electrical resistance, which was required to produce death). At the end of the exposure the rate of respiration in sea-water (at 16°C.) had fallen considerably below the normal. This might be expected, as the oxidases are usually injured or destroyed by heat.

Preliminary experiments in which the electrical resistance was determined showed that the tissue was killed by drying for 135 minutes in strong sunlight in a current of dry air. Pieces treated in this manner were washed for 15 minutes in sea water and the rate of respiration was then determined. It was found to be about five times the normal rate. In the course of about two hours it fell to the normal.

As it is well known that wounding,⁵ especially if severe, may cause a considerable rise in the respiration, it appeared advisable in this connection to make such experiments with *Laminaria*. The normal respiration in sea-water was first determined. After the tissue had been finely macerated (by means of a broken Pyrex glass-tube) on tested filter paper, it was rinsed from six to ten times with sea-water to free it of CO₂ and of any liberated pigment. The rate of respiration was then determined in sea-water. It was found that the injury caused a doubling of the rate which at the end of an hour was still above the normal. In this case the time of death could not be determined.

It is therefore evident that a considerable variety of killing agents raise the rate of respiration above the normal and that this increased rate may be maintained for some time after death. The fact that the rate eventually falls below the normal may be due to exhaustion of readily oxidizable materials or to destruction of oxidizing enzymes or to other causes.

That previous observers have not found a post mortem rate of respiration which is greater than the normal is probably due to the fact that the time of death was not accurately known and the observations were not commenced until the rate of respiration had sunk below the normal. It seems reasonable to suppose that if the rate of respiration is raised above the normal by an injurious agent it will not suddenly drop below the normal at the moment of death, but will decline gradually, as is the case in these experiments.

Summary.—The respiration of *Laminaria* may be much greater after death than in the normal condition. This is the case when it is killed by alcohol, acetone, ethyl bromide or formaldehyde as well as by wounding, drying and other means.

¹ Cf. Warburg, O., *Ergebn. Physiol.*, 14, 1914, (313).

² Haas, A. R., *Science, New York*, N. S., 44, 1916, (105).

³ This did not occur with low concentrations of these substances.

⁴ Osterhout, W. J. V., *Science, New York*, N. S., 35, 1912, (112); *Bot. Gaz., Chicago*, 61, 1916, (148). The determinations referred to in this paper were made in part by Professor Osterhout and in part by me.

⁵ Richards, H. M., *Ann. Bot., Oxford*, 10, 1896, (551). Czapek, F., *Biochemie der Pflanzen*, 2, 1905, (400 ff.).

THE MEANS OF LOCOMOTION IN PLANARIANS

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The ordinary locomotion of fresh-water planarians is of two types, gliding and crawling. True swimming movements are also used by the marine form, *Bdelloura*. When gliding, the planarian slips smoothly and evenly over some supporting surface, with little or no apparent muscular effort. It has been believed generally that this form of locomotion results chiefly, or even entirely from the beating of ventral cilia. Crawling* is accomplished through conspicuous muscular contractions.

Contrary to the opinion frequently expressed in papers on the histology of planarians, all species which I have so far examined have been found to be entirely covered externally with cilia. The cilia on the lateral margins of the anterior region beat in response to very weak stimuli. The cilia over most of the dorsal surface, on the lateral margins other than the head region, and on the ventral surface are usually inactive, except when subjected to strong mechanical or chemical stimuli. Long sensory hairs occur not only in the head region, but along the lateral margins and over the dorsal surface, as well. Tests with powdered carmine show that the ventral cilia of a gliding planarian are not beating during normal locomotion. On the other hand, a planarian when gliding on the under side of the surface film of water, so that the light falls upon its foot at an angle of about 45 degrees, and is reflected to the eye shows delicate muscular waves.

To determine whether locomotion could be accomplished either by the beating of cilia, or by muscular activity alone, a series of tests were made with solutions for the purpose of finding one that would inhibit muscular activity and leave the cilia free to beat normally, and another that would check ciliary action without interfering with muscular contractility. In either case, the animal must remain in all other ways as